

REVISIONS OF HYBOCHILUS AND GONIOCHILUS (ORCHIDACEAE)

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In the course of preparing a monograph of the onchioid orchid genus *Leochilus* Knowles & Westc. (Chase 1986c), the two species of the Central American genus *Hybochilus* Schltr. were collected and examined in order to determine their relationships to the species of *Leochilus*. Both these species have been rarely collected and are widely misunderstood. They have small, fleshy, complex flowers (especially *H. inconspicuus*) that are difficult to interpret once they are pressed and dried. This study thus benefits from the availability of live material. *Hybochilus inconspicuus* (Kränzlin) Schltr., the type species of *Hybochilus*, was found to be only distantly related to *Leochilus*, whereas *H. leochilinus* (Reichb. f.) Mansf. was determined to be a near relative. A number of significant features distinguish these two species, and these differences indicate that *H. leochilinus* cannot be maintained in *Hybochilus*. Additionally, it does not conform to the features of any other onchioid genus, and a new monotypic genus, *Goniochilus*, is proposed for this species.

MATERIALS AND METHODS

Herbarium specimens were borrowed from the following herbaria: F, G, K, MO, NY, SEL, US, and W. I also visited AMES and CR. Live material of *Hybochilus inconspicuus* from one locality and *Goniochilus leochilinus* from three localities in Costa Rica was also examined. The live plants were mounted on slabs of sassafras and grown in greenhouses at the Natural Sciences Building on the campus of the University of Michigan.

The illustrations in this paper were prepared from live material drawn with the aid of a drawing tube mounted on a dissecting stereomicroscope. Flowers and fruits of my numbered collections (MWC) were preserved in a modified FAA (53% ethanol, 37% water, 5% formaldehyde, and 5% glycerol). These will later be deposited in a major herbarium. When my collections represented new localities, specimens were pressed and deposited at CR and MICH. Pollinia were removed from live flowers, photographed on a Wild dissecting stereomicroscope, and then stored in gelatin medicine capsules. Scanning electron micrographs of the seeds were made on an Hitachi S570. All specimens were simply air dried before gold coating.

ECOLOGY AND DISTRIBUTION

Both *Hybochilus inconspicuus* and *Goniochilus leochilinus* are twig epiphytes and exhibit the features and traits associated with this habitat specialization (Chase 1986a, c). Like *Leochilus*, these two species move onto cultivated plants

and are more common than the paucity of collections would indicate. They have often been collected on *Citrus*, *Coffea*, and *Psidium guajava*. I did not observe either of them in primary forest, but I suspect, also like *Leochilus*, that they occur on small branches and twigs in the upper parts of the forest canopy. The localities I observed and the data from herbarium sheets indicate that they inhabit sites that never get as dry as those of some species of *Leochilus*. Cloud and moderate elevation rain forests (500–1500 m) appear to be their only habitat type, whereas *L. scriptus* (Scheidweiler) Reichb. f. also occurs on the seasonally dry Pacific side of Central America.

On cultivated plants, they may occur in relatively dense populations. I observed as many as 50 plants of *G. leochilinus* growing on single guava and orange trees in pastures (500 m) near Cariblanco (Alajuela Province), Costa Rica, in the Atlantic watershed. Similar numbers were also observed on guava in cloud forest (1500 m) near San Ramón (Alajuela Province), Costa Rica.

Oncidioid twig epiphytes are restricted to the outer branches of their hosts, and the rodriguezioid twig species (clade B; Chase 1986a) have a number of features associated with this habitat, including psygmoid habit (fanshaped with laterally flattened leaves and no pseudobulbs) in the seedling stage and elongate seeds with hooked ends (Chase 1986c). Lower chromosome numbers ($2n = 36-48$) also are associated with oncidoid twig epiphytism, but I made no counts for either of these species.

Many species that inhabit the trunks and other larger axes of their host take from five to seven years to reach maturity, but most of the oncidoid twig epiphytes do so in a single season (Chase 1986c). I did not observe these two species in a way that will permit me to state conclusively that they also have such speeded up life cycles, but they both exhibit the features observed for *L. labiatus* (Sw.) Kuntze and *L. scriptus* (Chase 1986c), which do have nearly an annual type of life history. These features are: blooming at small size and producing only a fraction of the number of flowers a large specimen produces; flowering on the first growth produced (they produce an annual sympodium; their age is the number of such growths present); ripening capsules in two to three months (*H. inconspicuus* only) instead of the typical ten to twelve; occurring in populations consisting of largely first-bloom plants; and only rarely living to be three or more years old.

I did not observe pollinators for either species, but their floral morphology and dull coloration suggests lower hymenopterans, much as was observed for *Leochilus* (Chase 1986b). *Leochilus* has a relatively open nectary that made access by polistine and polybiine wasps and halictid bees possible. They merely had to climb into the nectar cavity. Both *H. inconspicuus* and *G. leochilinus* have nectar cavities that are enclosed in such a way that I suspect access is only by the insect's tongue. In fact, they have a central groove that would guide the tongue into the nectary. The pollinarium may be attached to the mouth parts of the pollen vector of *H. inconspicuus* because of the relationship of the lip to the column and because the viscidium is long and narrow (the latter a feature that often occurs when the viscidium is attached to the tongue). The column-lip arrangement of *G. leochilinus* may result in pollinarium attachment on the thorax because, to gain access to the nectary, the insect would have to work its way a considerable distance into the channel in front of the cavity itself and probably contact the viscidium only when it backed out.

I observed only a small amount of nectar production in *G. leochilinus* and none in *H. inconspicuus*. Most of the species of *Leochilus*, however, do not produce nectar under greenhouse conditions, but those examined under field

conditions (seven of the nine species) all do so. My observations under cultivation may thus not be representative of what occurs in nature.

Both *Hybochilus* and *Goniochilus* are of restricted distribution; *H. inconspicuus* has been collected in the mountains around the Central Valley of Costa Rica and Chiriquí Province in western Panama, while *G. leochilinus* occurs in the Atlantic watershed and the Cordillera Central of Costa Rica, Nicaragua, and western Panama.

This distribution is typical of most genera of rodriguezioid orchids, which are all twig epiphytes. The group is more numerous and diverse away from the center of familial diversity in the Andes of South America. Of the larger grouping of related genera (discussed below), only *Konantzia* Dodson & N. H. Williams is Andean. *Capanemia* Barb. Rodr. is from southern Brazil, *Polyotidium* Garay and *Quekettia* Lindley are from northeastern South America, *Papperitzia* Reichb. f. is North American, and *Ionopsis* Kunth and *Trizeuxis* Lindley are found at lower elevations throughout the Neotropics, whereas *Leochilus* has the same general distribution as the last two genera but is most diverse in Central and North America.

Both *H. inconspicuus* and *G. leochilinus* are often microsympatric with *L. labiatus*. I observed the last growing with *G. leochilinus* on guava and orange trees near Cariblanco (Alajuela Province), Costa Rica, and a number of mixed collections indicate microsympatry for *L. labiatus* and *H. inconspicuus*. All three species occur near San Ramón (Alajuela Province), Costa Rica, but have not been collected at the same microsites. The flowering seasons of all three species overlap somewhat, but I have seen no putative instances of hybridization (I did not perform crossing experiments to determine if hybridization is possible).

COMPARATIVE MORPHOLOGY

Hybochilus and *Goniochilus* have a generalized oncidoid habit: ancipitous (two-edged, dorso-ventrally compressed), more or less globose pseudobulbs; conduplicate leaves; and laterally produced inflorescences. They may have one or two apical leaves and from one to five basal sheathing leaves that grade into a series of sheathing, basal bracts. They are small, caespitose herbs and have no unique vegetative features, although, once familiar with them, one can usually identify them in sterile or fruiting condition.

The seedlings of both species are psymoid, i.e., fanshaped with laterally flattened leaves and no pseudobulbs. This is the typical habit for seedlings of the rodriguezioid group, and they are often mistaken for small plants of the distantly related genus *Ornithocephalus* Hook., which has this same general habit. As the first season of growth is completed, flowering occurs concurrently with production of pseudobulbs and conduplicate leaves. Both *H. inconspicuus* and *G. leochilinus* make a complete transition to adult morphology, unlike *Macroclinium* Barb. Rodr. ex Pfitzer, *Plectrophora* Focke, and *Trizeuxis*, which retain, to varying degrees, the seedling habit into the adult stage.

The inflorescence of *H. inconspicuus* is an erect to pendent primary panicle, whereas that of *G. leochilinus* is always pendent and usually a raceme that may secondarily become paniculate. I use the term "primary" to indicate that the side branches are produced simultaneously with the main axis. In *Goniochilus*, *Leochilus*, and a number of other genera, the inflorescence is initially nearly always a raceme that will, if no or only a few fruits are set, initiate a series of lateral racemes. This is a primary raceme that may become secondarily paniculate. Robust specimens of this latter type may produce a weakly paniculate primary inflorescence.

The flowers of *H. inconspicuus* may be held with the lip lowermost, a position that is obtained by the twisting of the ovary if the inflorescence is erect. On pendent inflorescences, the flowers usually face downward, and the lip is nearest the axis, which is its position in bud. The flowers of *G. leochilinus* always face downward on a limp, pendent inflorescence. This flower position is rare in the oncioid orchids, although it is standard in other neotropical genera, such as *Stanhopea* Hook. *Leochilus oncioides* Knowles & Westc. also has a pendent inflorescence, but, in contrast, the flowers typically face outward with the lip lowermost.

The sepals and petals of both *H. inconspicuus* and *G. leochilinus* are abaxially carinate, but this is not a taxonomically useful feature since it occurs in most oncioid species. The lateral sepals are usually connate up to $\frac{3}{4}$ their length but may be free in the latter. This trait is also variably expressed within many other genera, such as *Leochilus*. In *G. leochilinus*, the bases of the lateral sepals are shortly adnate to the lip base.

The lip of *H. inconspicuus* is trilobate, with the lateral lobes basal and erect. The lip base forms a glabrous nectar cavity with an obscuring front wall adjacent to the bilobed lip callus. This type of lip morphology is similar to that of *Polyotidium* and is entirely different from that found in *Goniochilus* and *Leochilus*. In both these genera, the cavity is furnished with its own front wall (notched in some species of *Leochilus* and in *Goniochilus*), and the lip callus is a separate structure located somewhat forward of the nectary in *Leochilus* and much forward in *Goniochilus*. In *Goniochilus*, the notched front wall is covered with long hairs that obscure its presence.

The lip of *G. leochilinus* is also trilobate, but the lateral lobes are produced near the midpoint of the lip rather than at the base, as in *H. inconspicuus*, and do not form the nectary side walls. Additionally, the apical half of the lip is bent at a 90° angle relative to the basal portion. In both species, the midlobe is retuse.

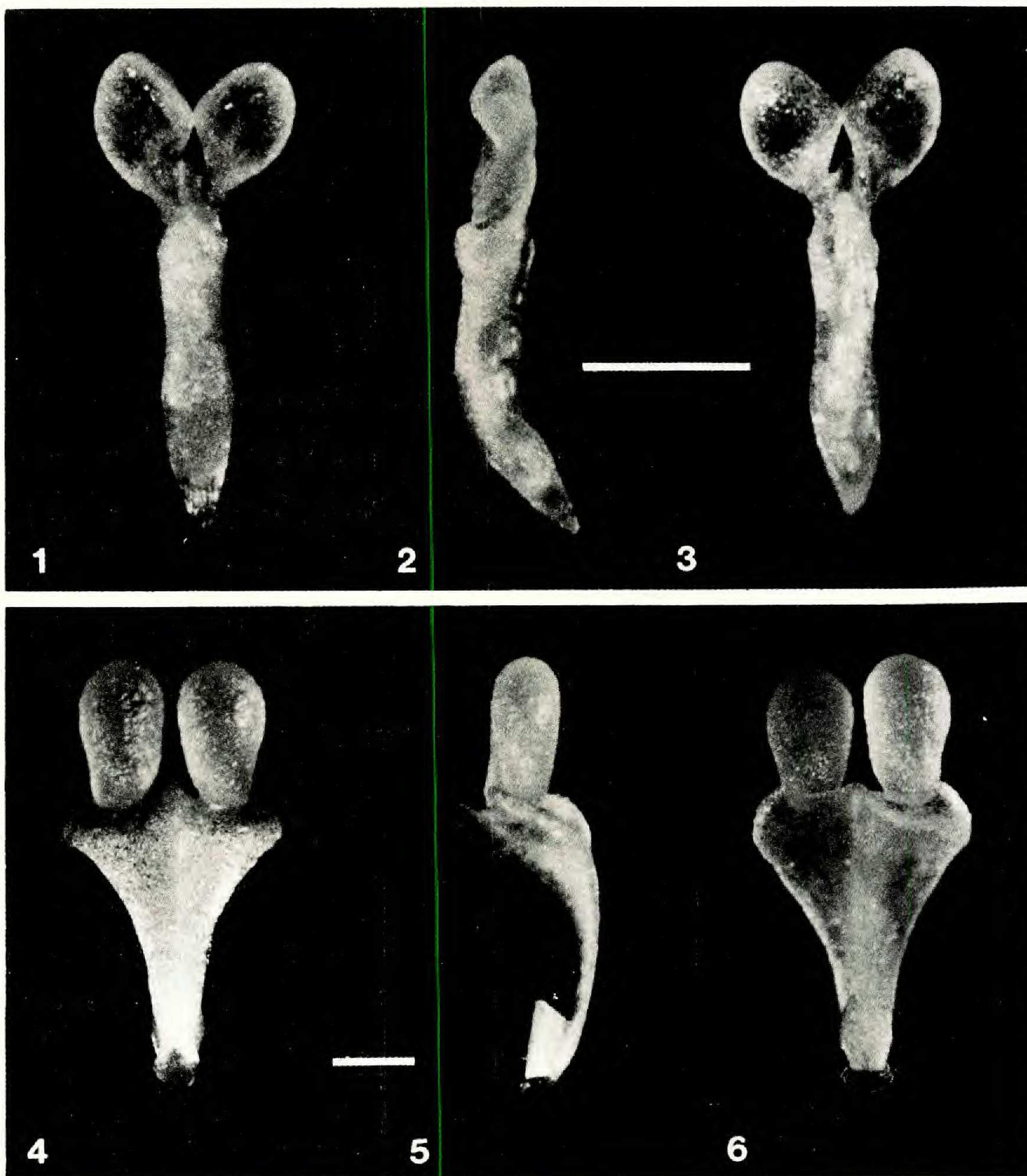
As is the case with most orchid genera, the column is of great systematic importance. These features in combination with lip morphology distinguish these two genera from their close relatives. Neither genus has a tabula infrastigmatica, as in *Oncidium* and its relatives, or a column foot, as in *Ionopsis*. The complex stigma of *H. inconspicuus* is located immediately below an elongate, bifurcated rostellum, and its opening is oriented perpendicularly to the column axis. The inner lobes of the bilobed stigmatic arms form a v-shaped groove. The short, bilobed, extrorse stigmatic arms are situated on the sides of the stigma. *Polyotidium* and some species of *Rodriguezia* have both stigmatic and column arms, but in *H. inconspicuus* the two parts appear to have the same origin and are in the same plane, so I consider them to be merely bilobed stigmatic arms rather than two sets of distinct arms.

In *G. leochilinus*, a more or less circular stigmatic cavity is located a short distance from the column apex, and the two, extrorse stigmatic arms are much longer and unlobed. In contrast, the stigma in *Leochilus* occurs nearly at the midpoint of the column, and the arms are perpendicular to the column axis.

The anther cap in *H. inconspicuus* is relatively long and hinged and is situated terminally on the apex of a short (only $\frac{1}{5}$ the length of the lip) column. In *G. leochilinus*, the anther cap is also elongate but unhinged. As in *Rodriguezia*, the anther of *G. leochilinus* is located dorsally on an elongate ($\frac{1}{2}$ the length of the lip) column and has a pronounced clinandrial protusion located below the stipe. This anther is not as dorsal as in *Notylia*, but it is much more so than in

Hybochilus and *Leochilus*. The substipular protrusion is also lacking in the latter two genera.

The pollinaria of *H. inconspicuus* and *G. leochilinus* are different from each other and distinctive among the rodriguezioid genera. The former has dorsoventrally flattened and twisted pollinia that are oriented in a plane corresponding with its narrow stigmatic opening. The great majority of onchioid species have globose pollinia and more or less circular stigmatic cavities. The major exception is *Notylia* and its close relatives, in which laterally flattened pollinia fit into a longitudinal stigmatic slit. The stipe of *H. inconspicuus* is slightly enlarged in the middle. Its head is somewhat tubularized, and the pollinia are inserted into two lateral depressions on its apex. This species also has a two-parted viscidium, but the proximal portion is not as well developed as in *Goniochilus* and *Leochilus*. The viscidium of *H. inconspicuus* is quite unusual among the rodriguezioid orchids in that it is nearly as long ($\frac{2}{3}$) as the stipe and has a pronounced ventral ridge that extends below the rostellum (Figs. 1-3).



FIGS. 1-6. Views of the pollinaria of *Hybochilus* and *Goniochilus*. 1-3. *Hybochilus inconspicuus*, Costa Rica (MWC84308). 1. Adaxial view. 2. Side view. 3. Abaxial view. 4-6. *Goniochilus leochilinus*, Costa Rica (MWC84210). 4. Adaxial view. 5. Side view. 6. Abaxial view. (Scale bar = 0.5 mm.)

The pollinarium of *G. leochilinus* has oblong pollinia inserted into two depressions on a greatly enlarged stipe head. The two parted viscidium of this species is oval and much shorter ($\frac{2}{3}$) than the stipe (Figs. 4–6).

The capsules of both species are typical of most rodriguezioid genera; i.e., they are deltoid, beaked, and dehisce by the three valves splitting along their edges and bending outward. The mature fruits of *H. inconspicuus* are short (1.0–1.5 cm) and only slightly beaked (0.2–0.3 cm), whereas those of *G. leochilinus* are much longer (3.5–4.0 cm) and more prominently beaked (0.8–1.0 cm).

The seeds of both species are typical of the rodriguezioid group. They are elongate and have prominent hooks on their ends, particularly the micropylar end (Figs. 7–10). The *Oncidium*-derived twig epiphytes, the “variegata oncidiums,” have a similar elongate shape, but their testa extensions are knobbed rather than hooked (Figs. 11, 12). This difference supports the contention (Chase 1986a) that these two groups have an independent origin.

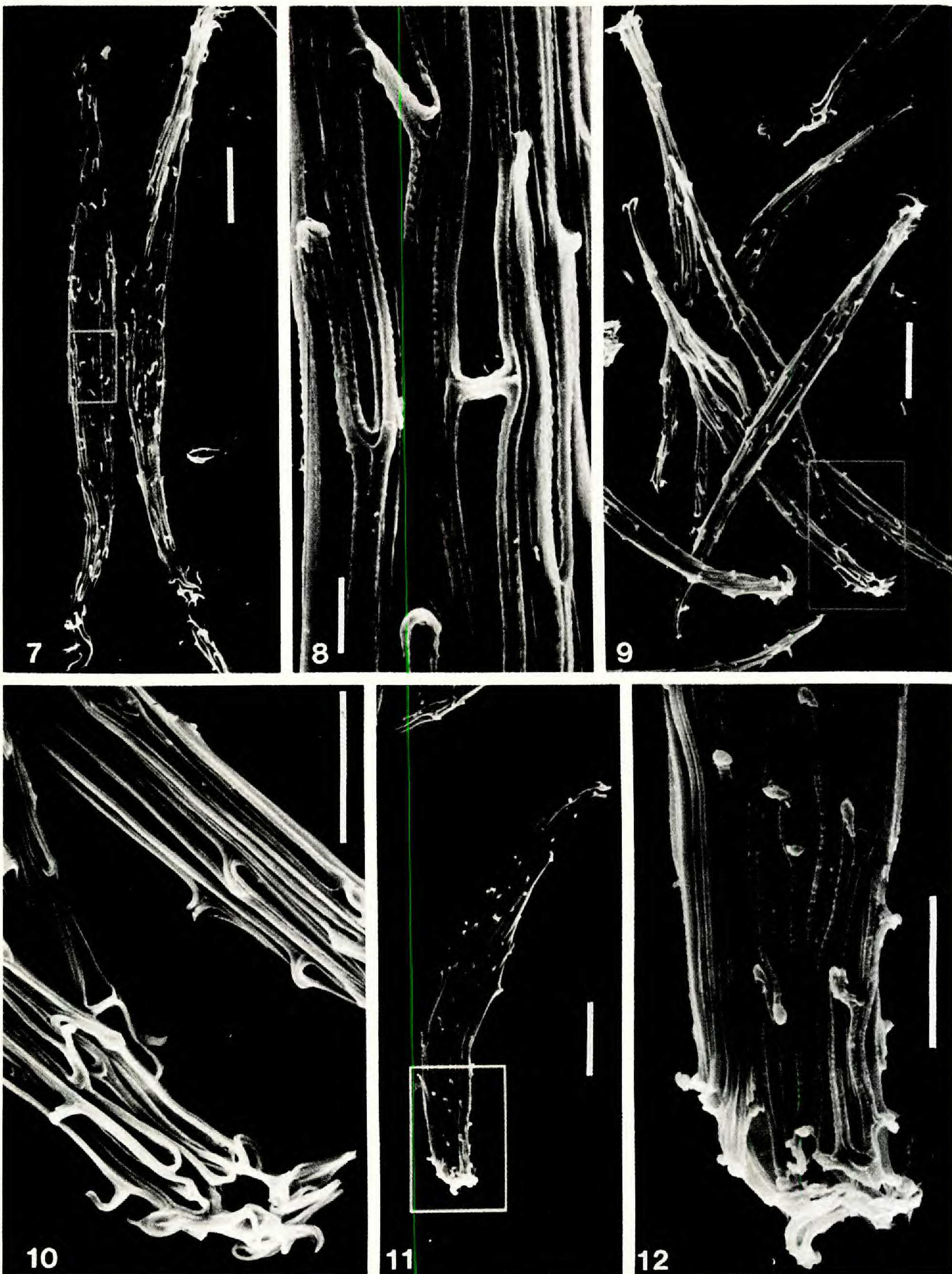
Not all small oncidoid species that occasionally occur on twigs are twig epiphytes. *Rhyncostele pygmaea* (Lindley) Reichb. f., a species as diminutive as *H. inconspicuus* and *G. leochilinus*, may grow, under certain environmental conditions, on smaller axes of its hosts, but it then occurs on limbs of all sizes. This species belongs to the trunk-limb genera related to *Odontoglossum* Kunth and *Oncidium* Sw. (clade A; Chase 1986a), and it has the seeds typical of this group. They are much wider for their length than those of the twig epiphytes and lack the prominent testa extensions (Figs. 13, 14).

Summary. The taxonomically significant features of *Hybochilus*, *Goniochilus*, and the other rodriguezioid genera I consider their closest relatives are presented in table 1. The important features of *H. inconspicuus* are: a glabrous lip nectary that is enclosed in front by a bilobed callus; a lack of lateral sepal-lip adnation; a short column with short bilobed stigmatic arms; a narrow stigmatic opening; a terminal anther; and a pollinarium with dorsoventrally flattened pollina, an indented stipe head, and an elongate, weakly biparted viscidium. *Goniochilus leochilinus* is distinguished from its close relatives by: a shallow nectary with a grooved, pubescent entry channel; a lip callus situated much in front of the nectar cavity; a bent lip; a degree of lateral sepal-lip adnation; an elongate column with extrorse, stigmatic arms; a dorsally situated anther with a substipular protuberance; and a pollinarium with a greatly enlarged, indented stipe head and a small, strongly biparted viscidium.

GENERIC RELATIONSHIPS

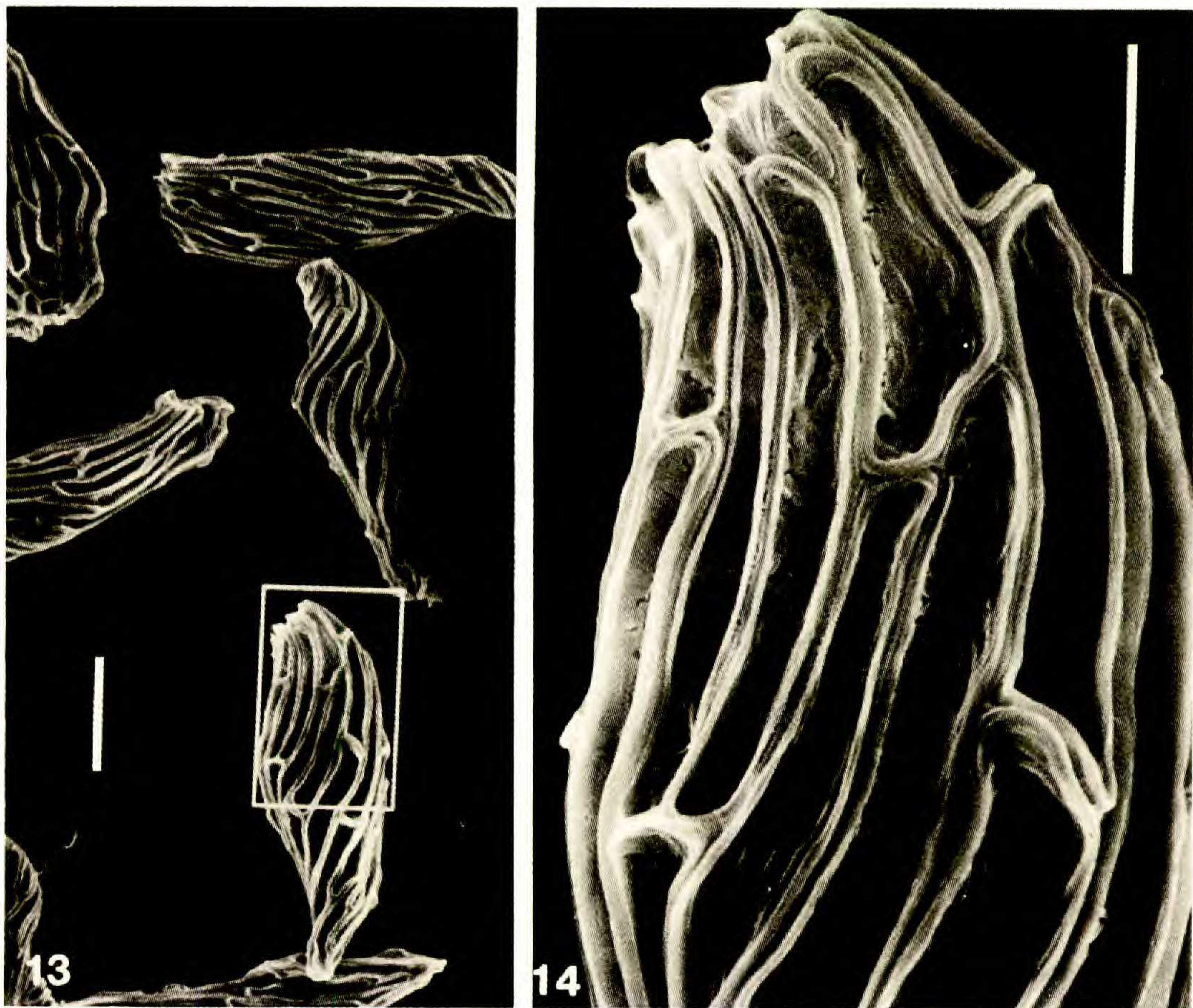
Hybochilus and *Goniochilus* clearly belong to the rodriguezioid group of the oncidoid orchids. This is a heterogeneous group that has a dimorphic life history (psygmoid seedlings and conduplicate-leaved, pseudobulb-bearing adults) and flowers that lack the complex calli and tabula infrastigmatica of *Oncidium* and its relatives. Within the rodriguezioid group, at least three evolutionary subgroupings occur, and *Hybochilus* and *Goniochilus* belong to the one (table 2) that does not have the nectar horns of *Rodriguezia*, *Comparettia* Peoppig & Endl., and their relatives or a stigmatic slit that parallels the column, as is found in *Macradenia* R. Br., *Notylia*, and their relatives.

Many of the rodriguezioid genera are monotypic and may be considered true “oddities.” *Erycina* Lindley, *Papperitzia*, *Polyotidium*, *Saundersia* Reichb. f., and *Trizeuxis* are difficult to ally closely to any other single genus. Other genera, such



FIGS. 7–12. Seed morphology of twig epiphytes. 7, 8. *Hybochilus inconspicuus*, Costa Rica (Alfaro s.n.; US). 7. Whole seeds. 8. Testa cell morphology. 9, 10. *Goniochilus leochilinus*, Costa Rica (MWC84371). 9. Whole seeds. 10. Hooks on micropylar end. 11, 12. *Oncidium urophyllum* Lindley, Dominica (Wilbur et al. 7668; MICH). 11. Whole seed. 12. Testa extensions on micropylar end. (Scale bar = 0.1 mm in all except 8; in 8, scale bar = 0.01 mm.)

as *Capanemia* and *Quekettia*, are heterogeneous “catch-alls,” and contain species, such as *C. superflua* (Reichb. f.) Garay and *Q. vermueleniana* Determann that appear to represent additional new genera with different affinities from those now considered congeneric.



FIGS. 13, 14. Seed morphology of a trunk-limb species, *Rhyncostele pygmaea*, Mexico (MWC82125; MICH). 13. Whole seeds. 14. Testa cell morphology. (Scale bar = 0.1 mm.)

I consider *Hybochilus* to be allied to *Capanemia*, *Konantzia*, *Polyotidium*, *Quekettia*, and *Trizeuxis*. Its nectary type also occurs in *Polyotidium*, and its pollinarium form is similar to those of *Polyotidium* and *Trizeuxis*, but the flattened, twisted pollinia are unique.

Goniochilus is, as stated earlier, most closely related to *Leochilus*. They both have shallow nectaries that are distinct from the lip callus. The pollinaria of these two genera are similar to each other and to that of *Papperitzia*, although the last has a much more complex floral morphology. *Goniochilus leochilinus* could be considered merely a pendently flowered species of *Leochilus*, but none of its important features occur in any species of *Leochilus*. More importantly, their shared structures are typical of many rodriguezioid genera.

Even though *Hybochilus* and *Goniochilus* have distinctly different floral morphologies from any other rodriguezioid genus, I am loath to create two more monotypic genera. I cannot envision how these fit into any evolutionary pattern except as completely isolated end points that have as their ancestor something similar to *Rodriguezia*. The differences between any of these genera and *Rodriguezia* are, however, numerous and drastic. The alternative to establishing *Goniochilus* is to consider all these species as members of an extremely heterogeneous supergenus (one more diverse than any other orchid genus with which I am familiar).

In contrast to the clearly delineated rodriguezioid group are the oncioid trunk-limb genera (clade A; Chase 1986a). Among these, one has to search diligently to find generic distinctions that do not have intermediates or species that express mixtures of the generic characteristics. Even the closest relatives of

Table 1. Comparison of the genera most closely related to *Hybochilus* and *Goniochilus* (tentatively arranged into four informal alliances).

	anther position	column length	stigmatic arms	lip-lateral sepal adnation	nectar cavity	stigmatic opening
<i>Goniochilus</i>	dorsal	long	extrorse	+	lip base	circular
<i>Leochilus</i>	terminal	long	perpendicular	+	lip base	circular
<i>Papperitzia</i>	dorsal	short	extrorse	+	lip base	elongate scooped
<i>Capanemia</i>	terminal	short	extrorse	-	-	circular
<i>C. superflua</i> group	dorsal	short	extrorse	-	lip base	circular
<i>Hybochilus</i>	terminal	short	bilobed, extrorse	-	lip base*	narrow
<i>Konantzia</i>	terminal	long	none	-	-	circular
<i>Polyotidium</i>	dorsal	long	extrorse	-	lip base*	elongate scooped
<i>Quekettia</i>	terminal	long	introrse, extrorse	-	-	circular
<i>Trizeuxis</i>	terminal	long	none	-	-	v-shaped
<i>Ionopsis</i>	terminal	long	none	-†	lateral sepals	circular
<i>Rodriguezia</i> (<i>maculata</i> group)	dorsal	long	extrorse	-	-	circular
<i>Q. vermueleniana</i>	dorsal	long	extrorse	+	lip base	v-shaped

*lip callus forms part of nectary front wall.

†sepals adnate to column foot.

Hybochilus and *Goniochilus* are easy to distinguish, but this cannot be said of *Miltonia* Lindley, *Odontoglossum*, and *Oncidium*.

Of the 18 genera I consider members of the group to which *Hybochilus* and *Goniochilus* belong, 44% (8) are monotypic and another 28% (5) comprise only two species (table 2). I suspect that, once revisionary work is undertaken, the number of monotypic genera will increase substantially because superficially similar species have been lumped in a number of cases.

I do not believe that the high number of small genera is a result of the orchid taxonomist's "splitting" nature. Instead, I suspect this plethora of "oddballs" may be a correlative of twig epiphytism. This extreme and depauperate habitat (Chase 1986a) requires a high degree of specialization, and many, highly specialized groups are low in number. The rodriguezioid twig epiphytes have approximately 190 species, while their relatives that inhabit the trunks and other larger axes have 800 (Chase 1986a). In spite of the disparity in numbers, the number of monotypic genera in each group is nearly the same (17 and 16, respectively).

TAXONOMIC HISTORY

At various times, three species have been placed in *Hybochilus*. The first of these to be described was *Goniochilus leochilinus*. Reichenbach fil. published a relatively nonspecific description of it in 1871 and placed it in *Rodriguezia*. In particular, he mentioned that it was similar to the nectaryless members of that genus, specifically "*R. maculata*," which I assume to be *R. maculata* (Lindley) Reichb. f., rather than *R. maculata* Lindley (= *Leochilus oncidioides*). Reichen-

Table 2. Rodriguezioid genera in the same subgrouping as *Hybochilus* and *Goniochilus*.

	number of species
<i>Antillanorchis</i> Garay	1
<i>Capanemia</i> Barb. Rodr.	15
* <i>Erycina</i> Lindley	1
<i>Hybochilus</i> Schltr.	1
<i>Ionopsis</i> Kunth	5
<i>Goniochilus</i> M. W. Chase	1
<i>Konantzia</i> Dodson & N. H. Williams	1
<i>Leochilus</i> Knowles & Westc.	9
<i>Papperitzia</i> Reichb. f.	1
<i>Plectrophora</i> Focke	4
<i>Polyotidium</i> Garay	1
<i>Quekettia</i> Lindley	6
<i>Rodriguezia maculata</i> (Lindley) Reichb. f. group	9
<i>Rodrigueziopsis</i> Schltr.	2
<i>Sanderella</i> Kuntze	1
<i>Saundersia</i> Reichb. f.	2
<i>Trizeuxis</i> Lindley	1
<i>Warmingia</i> Reichb. f.	2

*I consider *Erycina diaphana* Reichb. f. a synonym of *Oncidium hyalinobulbon* Llave & Lex. and a member of *Oncidium* Sw. allied to *O. cheiroporum* Reichb. f. The removal of this species leaves *Erycina* with only the type species, *E. echinata* Lindley.

bach failed to note a number of important features of this species, such as the presence of a nectary and the dorsally situated anther. The identity of this taxon was not ascertainable from the description, and the species was to remain poorly known to orchidologists until new collections were sent from Costa Rica in the 1920's.

In 1895, Kränzlin described *H. inconspicuus*, also in *Rodriguezia*. Probably for much the same reason as Reichenbach, Kränzlin allied his new species to those of *Rodriguezia* that lack a nectar spur. The latter also have a trilobed lip, but they lack a nectary altogether, and *H. inconspicuus* has a well-developed one formed by the lip base.

That neither of these species had real similarity to *Rodriguezia* did not escape Schlechter, and he stated so when he established *Hybochilus* (1920) as a monotypic genus based on *R. inconspicua* Kränzlin. He allied his new genus with *Trizeuxis*. At that time, Schlechter had not seen material of *Rodriguezia leochilina* Reichb. f., but he did have a sketch sent by Zahlbruckner and Keissler from the Reichenbach herbarium. This drawing did not furnish him with the necessary information, and he left matters as they were, mentioning that *R. leochilina* might represent a second species of *Hybochilus*.

When Schlechter did receive material of *R. leochilina* in 1923, he transferred it, not into *Hybochilus*, but rather into *Mesospinidium* Reichb. f. He apparently saw no reason to place it in *Hybochilus*, but his comments about the transfer indicate confusion over the concept of *Mesospinidium*, which has had a history of being misunderstood. It has often been a "catchall" for species that did not fit well anywhere else. After Schlechter's death, Mansfeld (1938) made the combination in *Hybochilus*, and since it obviously did not belong in *Mesospinidium*, the transfer has been accepted by most later authors.

Before the transfer of *R. leochilina*, Mansfeld (1934) had described a third species and placed it in *Hybochilus*. This entity, *H. huebneri*, was a great deal more similar to *H. inconspicuus* than is *G. leochilinus*, but it too is not closely related. Mansfeld was quite aware of the great number of differences between his new species and *H. inconspicuus*, but he chose not to create for it a new genus. Garay (1958) segregated *H. huebneri* into the monotypic genus *Polyotidium*. Now, with the splitting off of *H. leochilinus*, all three species that have been described as members of *Hybochilus* are placed in monotypic genera.

TAXONOMY

KEY TO FLOWERING AND FRUITING SPECIMENS OF HYBOCHILUS AND GONIOCHILUS

Inflorescence a compound panicle, erect to pendent; flowers 0.3–0.35 cm long; lip with a glabrous, basal nectar cavity with the front wall flush with the callus; stigma located immediately below the forked rostellum and bordered by two, short, bilobed stigmatic arms; anther terminal; pollinia dorsoventrally flattened; capsules 1.0–1.5 cm long with a beak 0.2–0.3 cm long.

Hybochilus inconspicuus.

Inflorescence a weak, pendent raceme (rarely a simple panicle); flowers 1.0–1.8 cm long; lip with a basal nectar cavity with a pilose, notched front wall and a lip callus situated much in front of the nectary; stigma more or less a circular cavity located near the column apex, with two, long, unlobed stigmatic arms; anther dorsal; pollinia globose; capsule 3.5–4.0 cm long with a beak 0.8–1.0 cm long.

Goniochilus leochilinus.

Hybochilus Schltr., Repert. Spec. Nov. Regni Veg. 16: 429. 1920.—TYPE: *Hybochilus inconspicuus* (Kränzlin) Schltr.

Small to medium-sized, short-lived, perennial, caespitose herbs epiphytic on small branches and twigs, with the pseudobulbs clustered on short, creeping rhizomes. Pseudobulbs ovoid to suborbicular, ancipitous, unifoliate or bifoliate, often both conditions present in the same population or even in the same individual, lower portions concealed by 2 or 3 sheathing leaves, uppermost larger, eventually deciduous. Leaves elliptic-lanceolate, coriaceous, glabrous, conduplicate, with an unequally bilobed apex, margins entire, eventually deciduous. Inflorescences produced laterally from the base of a pseudobulb, subtended by a sheathing leaf, moderate to long, primarily a complex panicle, erect to pendent, stiff, many-flowered. Pedicellate ovaries twisted or not, glabrous. Flowers small to minute, weakly colored, inconspicuous, resupinate to pendent. Dorsal sepal free, laterals united up to $\frac{3}{4}$ their length, all sepals subequal, narrowly ovate, dorsally carinate, shortly acuminate, with entire margins. Petals free, similar to and connivent with the sepals; lip broadly attached to the column, forming a basal nectar cavity, exceeding the other perianth parts, trilobed, the sidelobes basal, erect and partially enfolding the column, with a fleshy, glabrous, bilobed callus fused with and partially forming the nectary front wall. Column short, with 2, short, bilobed, extrorse stigmatic arms at the column apex, the base without a foot; stigmatic cavity immediately below the long, forked rostellum, narrow, perpendicular to the column axis; clinandrium truncate; anther terminal, operculate, incumbent, 1-celled; anther cap oblong in outline, hinged; pollinarium with 2 waxy, dorsoventrally flattened pollinia, attached into 2 depressions on the stipe head by abundant, irregularly shaped viscin (caudicles); viscidium elongate, nearly as long as the stipe, bilobed, the proximal much smaller; stipe long, narrow, somewhat inflated in the middle, somewhat tubularized, the head narrow, with two depressions. Capsules deltoid, weakly carinate, with a short beak and persistent perianth. Seedlings psygmoid and pseudobulbless; pseudobulbs developing at maturity, usually at the end of the first season of growth.

Hybochilus inconspicuus (Kränzlin) Schltr., Repert. Spec. Nov. Regni Veg. 16: 430. 1920. *Rodriguezia inconspicua* Kränzlin, Bull. Herb. Boissier 3: 630. 1895.—TYPE: COSTA RICA. San José Prov., "from the Botanical Institute," without specific locality, fl, *Tonduz s.n.* (holotype: G!).

Rodriguezia candelariae Kränzlin, Bot. Jahrb. Syst. 54, Beibl. 117: 32. 1916.—TYPE: COSTA RICA. San José Prov., Candelaria-Gebirge, *Hoffmann s.n.* (holotype: B, destroyed).

Leochilus parviflorus Standley & L. O. Williams, Ceiba 1: 235. 1951.—TYPE: COSTA RICA. Alajuela Prov., Carrizal, 1500 m, fl, 12 March 1950, *Leon 2325* (holotype: US, photo!; isotype: MO!).

Epiphytic herbs up to 10 cm tall, often blooming at small sizes. Pseudobulbs prominent, suborbicular to oval in outline, wrinkled at maturity, 0.8–2.8 cm tall, 0.7–1.2 cm wide. Leaves 1, rarely 2 per pseudobulb, elliptic-lanceolate, 3.5–9.0 cm long, 0.8–1.8 cm wide. Inflorescences 1, 2, or rarely more, erect to pendent, produced on a mature growth, 6.0–40.0 cm long, bearing 30–150 minute flowers, each node and peduncle covered by a bract, those on nodes 5–17 mm long, those on peduncles 2–3 mm long, often with partially developed or aborted lateral

branches in the proximal 3–5 nodes. Pedicellate ovaries 3–4 mm long. No fragrance detected. Dorsal sepal free, laterals fused up to $\frac{3}{4}$ their length, green-cream with red to red-purple suffused margins, 2.5–3.0 mm long, 1.5–2.0 mm wide. Petals whitish with red-purple margins, 2.5–3.0 mm long, 2.0 mm wide; lip whitish, with a green-yellow spot and red to red-purple maculations in front of the callus, trilobed, the midlobe somewhat concave, retuse, 3.5–5.0 mm long, 1.5–2.0 mm wide; nectary glabrous with high walls; lip callus a deeply bilobed, elongate pad, higher near nectary, covering $\frac{1}{2}$ of lip lamina, glabrous. Column whitish, 0.5–1.0 mm long, 1.0 mm in diameter; anther cap cream; pollinia yellow; stipe elongate with a wedged apex; viscidium golden-brown with a raised center ridge. Capsule carinate, shortly beaked, 1.0–1.5 cm long (including beak), 0.5–1.0 cm in diameter. Fig. 15.

Phenology. Flowering occurs from January through June but is concentrated in February–March. The fruits appear to mature rapidly, and dehiscing capsules occur on plants collected as early as May. These surely represent the fruits set that same year and not those of the previous season because no new sympodium is evident as one would expect if the fruits took one year to mature [the latter is the pattern observed in those species of *Leochilus*, such as *L. crocodiliceps* Reichb.f. and *L. tricuspидatus* (Reichb. f.) Kränzlin, that require twelve months to mature].

Habitat. *Hybochilus inconspicuus* grows on twigs and small branches in cloud forest regions of 1000 to 1500 m. It often occurs on introduced and cultivated plants, on which it may be locally abundant.

Distribution. This species is largely confined to the mountains surrounding the Central Valley of Costa Rica (Fig. 16). This is the same general range exhibited by *Leochilus tricuspидatus*, a species once collected in western Panama; *H. inconspicuus* has been found there as well (Dressler & N. H. Williams, pers. comm.).

REPRESENTATIVE SPECIMENS. COSTA RICA. Alajuela: Naranjo, orilla del Río Colorado, 925–950 m, fl, 7 Apr 1921, *Brenes 11* (AMES, NY); near San Ramón, fl, Jul 1941, *Brenes 23212a* (NY); Carrizal (purch. from street vendor in San José), fl, 23 Feb 1984, *Chase 84305* (CR, MICH). San José: Vicinity of San José, sterile (mixed collection of *H. inconspicuus* and *Leochilus labiatus*), Feb 1924 (AMES); orillas del Río Virilla, entre Heredia y San José, fl, Jun 1931, *Brenes 14299a* (NY); Río Tirribí, near San José, fl, 10 Feb 1924, *Alfaro 33966* (AMES); vicinity of La Verbena, 1200 m, fl, 29 Jan 1924, *Standley 32246* (AMES). Cartago: El Muñeco, S of Navarro, fl, 8–9 Feb 1924, *Standley 33706* (AMES).

This species is difficult to confuse with any other. The combination of a compound panicle, minute, distantly spaced flowers, and a short, complicated column immediately identify it. In Central America, only *Trizeuxis falcata* Lindley has similar small flowers, but they are densely packed (almost into heads), and the plant is psygmoid and lacks well-developed pseudobulbs. *Konantzia minutiflora* Dodson & N. H. Williams from Ecuador is also similar but has an elongate, wingless column and an aborted apical leaf.

Rodriguezia candelariae (for which no type exists) was described by Kränzlin as distinct from *R. inconspicua* on the basis of a smaller flower, a pendent inflorescence, and the presence of abortive lateral branches positioned at the lower lateral buds. Interestingly, he stated that the flowers of this new species were 4 mm long, whereas the length he gave for *R. inconspicua* was 3 mm. The inflorescence habit appears to be variable among plants in the same population, and the

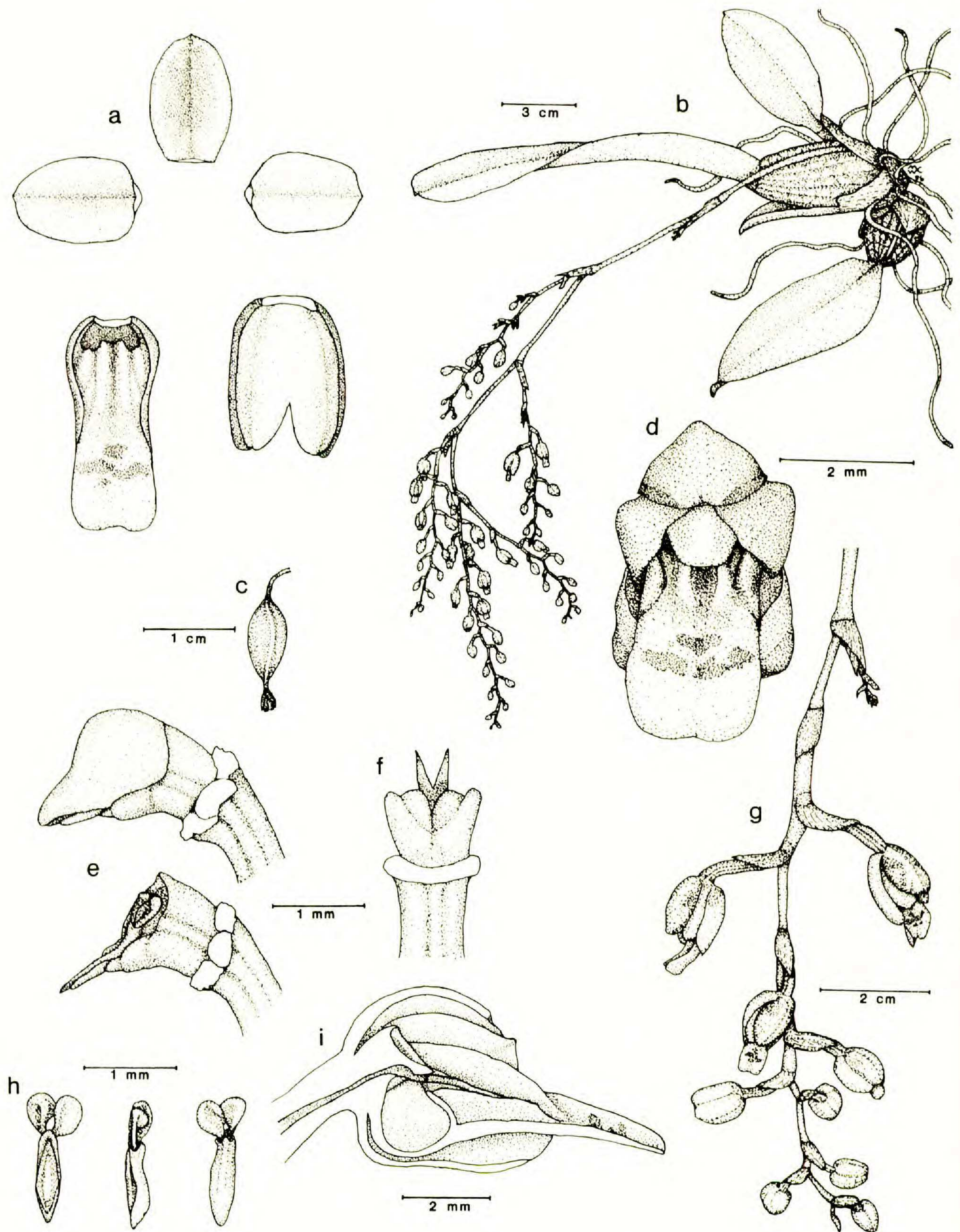


FIG. 15. *Hybochilus inconspicuus*, Costa Rica (MWC84308). a. Perianth parts. b. Habit. c. Capsule. d. Flower, front view. e. Column, side views; with anther cap (top) and with anther cap removed (bottom). f. Column, ventral view. g. Inflorescence habit. h. Pollinarium, three views (l. to r.): abaxial, side, and adaxial. i. Flower, longitudinal section.

abortive lateral branches occur on almost all specimens. Therefore, I consider this to be a typical variant of the earlier concept. Schlechter, who examined Kränzlin's original material, reached the same conclusion (1920).

In the original description of *R. inconspicua*, Kränzlin listed as a synonym *Trichocentrum candidum* Lindley, which was based on material from Guatemala.



FIG. 16. Distribution of *Hybochilus inconspicuus* and *Goniochilus leochilinus* in southern Central America (southern Nicaragua, Costa Rica, and western Panama).

He stated that, in spite of two discrepancies (which he explained away), Lindley's concept was surely the same as his. He could not, of course, transfer the epithet to *Rodriguezia* because *candida* was already occupied in that genus, and so he gave the species a new name with a new type (the type of *T. candidum* is in the

Lindley Herbarium). This species is not at all similar to Kränzlin's *R. inconspicua* and is a member of *Trichocentrum*, even though it does lack the elongate spur that occurs in most species of that genus.

The epithet *inconspicua* undoubtedly refers to the remarkably small flowers of this species. In Central America, only *Trizeuxis falcata* among the onchioid species is as small, but a number of genera in South America (*Capanemia*, *Konantzia*, *Quekettia*, among others) have flowers as small or smaller.

Goniochilus M. W. Chase, gen. nov.—TYPE: *Goniochilus leochilinus* (Reichb. f.) M. W. Chase.

Planta epiphytica parvaque habitu *Leochili labiati* (Sw.) Kuntze et pseudobulbis ovoideis et apicaliter unifoliatis. Folia crassa carnosaque. Inflorescentia lateralis, pendula, racemosa vel rarerer paniculata. Flores cernui. Labellum trilobum, nectario basali et apice perpendiculariter flexo. Columna apoda duobus brachiis stigmaticis et anthero semidorsali. Pollinia duo. Stipes amplificatus apicaliter. Viscidium bipartitum.

Small to medium-sized, short-lived, perennial, caespitose herbs, epiphytic on small branches and twigs, with pseudobulbs clustered on short, creeping rhizomes. Pseudobulbs ovoid to suborbicular, ancipitous, unifoliate, lower portions concealed by 2 to 3 sheathing leaves, uppermost larger, eventually deciduous. Leaves elliptic-lanceolate, coriaceous, glabrous, conduplicate, with an unequally bilobed apex, margins entire, eventually deciduous. Inflorescences produced from base of pseudobulb, rarely apically, subtended by a sheathing leaf, moderate to long (for the size of the plant), primarily racemose to weakly paniculate, often secondarily paniculate, pendent, many-flowered. Pedicellate ovaries glabrous, not twisted. Flowers small, weakly colored, inconspicuous, pendent. Lateral sepals free to united up to $\frac{2}{3}$ their length, shortly adnate to the lip base, all sepals subequal, elliptic, dorsally carinate, shortly acuminate to obtuse. Petals free, smaller than sepals, narrowly ovate to oblanceolate, obtuse, forward projecting, concealing column; lip broadly attached to base of column, forming a nectar-secreting cavity, greatly exceeding other perianth parts, trilobed above the middle and bent at a 90° angle to the base, the lip exclusive of the nectary glabrous. Column moderately long, with 2 extrorse stigmatic arms near the anther, the base without a foot; stigma a simple more or less circular cavity; clinandrium truncate, with a prominent protuberance under the stipe; another more or less dorsally situated, operculate, incumbent, 1-celled; anther cap oblong in outline, unhinged; pollinarium with 2 waxy pollinia, with a curving suture on the abaxial side, attached to 2 lateral depressions in the stipe head with abundant, irregularly shaped viscin (caudicles); viscidium oval, distinctly biparted, the stipe with undercurled edges, with a cupshaped, much broadened head and a prominent dorsal protuberance. Capsules deltoid, weakly carinate, with a pronounced beak and persistent perianth. Seedlings psygmoid and pseudobulbless; pseudobulbs developing at maturity, often at the end of the first season of growth.

The genus is named in reference to the lip with the apical half bent at a 90° angle relative to the basal portion.

Goniochilus leochilinus (Reichb. f.) M. W. Chase, comb. nov. *Rodriguezia leochilina* Reichb. f., Gard. Chron. 1: 970. 1871. *Mesospinidium leochilinum* (Reichb. f.) Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 253. 1923. *Hybochilus leochilinus* (Reichb. f.) Mansf., Repert. Spec. Nov. Regni Veg. 44: 58. 1938.—TYPE: COSTA RICA. Without specific locality, collector unknown, “flowered in the Royal Exotic Nursery of Messrs. Veitch & Sons” (holotype: W!).

Epiphytic herbs up to 15 cm tall, often blooming at small sizes in the first year of growth, typically red-purple suffused throughout. Pseudobulbs usually prominent, strongly ancipitous, suborbicular to oval in outline, 0.6–2.0 cm tall, 1.0–1.5 cm wide. Leaves nearly always 1 per pseudobulb, narrowly elliptic-lanceolate, 2.5–14.0 cm long, 0.6–2.4 cm wide, with a well-developed conduplicate petiole. Inflorescences 1, 2, or rarely more, weak, pendent, produced on a mature growth, zigzag, 7.0–45.0 cm long, bearing 5–60 flowers, each node and peduncle covered by a bract 3–12 mm long, those covering lateral buds much larger. Pedicellate ovaries 4–6 mm long. Flowers sweetly fragrant. Dorsal sepal free, lateral sepals free to fused up to $\frac{2}{3}$ their length, green-yellow, with large red-brown to brown maculations, 6–9 mm long, 4–5 mm wide. Petals similar, 5–8 mm long, 3–4 mm wide; lip white with red to rose-red spots in front of the callus, midlobe subquadrate, convex, retuse, side lobes broadly triangular, whole lip 10–13 mm long, 4–6 mm wide across the lateral lobes; nectary shallow with a densely pilose throat; lip callus a raised rectangular, sulcate pad, higher toward the lip base, situated much in front of the nectary, more or less glabrous to slightly papillose. Column whitish with red markings, 5–7 mm long, 1–2 mm in diameter; anther cap cream; pollinia yellow, ovoid. Capsule weakly carinate with an elongate beak, 3.0–4.5 cm long (including beak), 1.0–1.5 cm in diameter. Fig. 17.

Phenology. Flowering in *Goniochilus leochilinus* occurs from late September to early January, but is concentrated in October and November. Fruit maturation appears to take ten to twelve months, and dehiscence takes place shortly before the next season's flowering.

Habitat. This species grows on twigs and other smaller branches of woody plants in cloud and rain forests. Its elevational range is from 500 to 1500 m. As is true of most twig epiphytes, *G. leochilinus* moves onto introduced and cultivated plants, especially *Citrus*, *Coffea*, and *Psidium guajava*, on which it may be locally abundant.

Distribution. This species has been collected in the Cordillera Central and the Atlantic watershed of Costa Rica and Nicaragua (Fig. 16). It also has been reported from western Panama (Dressler & N. H. Williams, pers. comm.).

REPRESENTATIVE SPECIMENS. NICARAGUA. Jinotega: Jinotega Grande, 1350 m, fl, *Heller 4232* (SEL). Matagalpa: Finca El Roblar, 850 m, fl, *Heller 3977* (SEL); Cordillera Central de Nicaragua, 4–6 km N of Santa María de Ostuma, 1500–1600 m, fl, 28 Nov 1973, *Williams & Molina R. 42517* (F); Finca La Harmonía, 1300 m, fl, *Heller 3308* (SEL).—COSTA RICA: Guanacaste: Los Ayotes, near Tilarán, 600–700 m, sterile, 21 Jan 1926, *Standley & Valerio 45438* (AMES). Alajuela: San Pedro de San Ramón, 1200 m, fl, June 1921 (AMES), and Cerro de San Rafael de San Ramón, 1275 m, fl, 25 Nov 1921 (NY), *Brenes 193*; San Isidro de San Ramón, 1050 m, fl, 12 Nov 1923, *Brenes 2992* (NY); 20 km from San Ramón exit off Interamerican Hwy on rd to La Paz, 84°34'W, 10°10'N, 1200 m, fr, 19 Mar 1984, *Chase 84371* (CR, MICH); Virgen del Socorro, 800 m, fl (buds only), 15 Sept 1979, *Luer, Luer, & Walter 4173a* (SEL). San José: beside Río La Hondura, 1050 m, fl, early fr, 5 Dec 1971, *Lent 2285* (AMES, F, MO). Limón: lago sin nombre al pie de Fila Lleskila, 1160 m, fl, 4 Nov 1984, *Gómez*

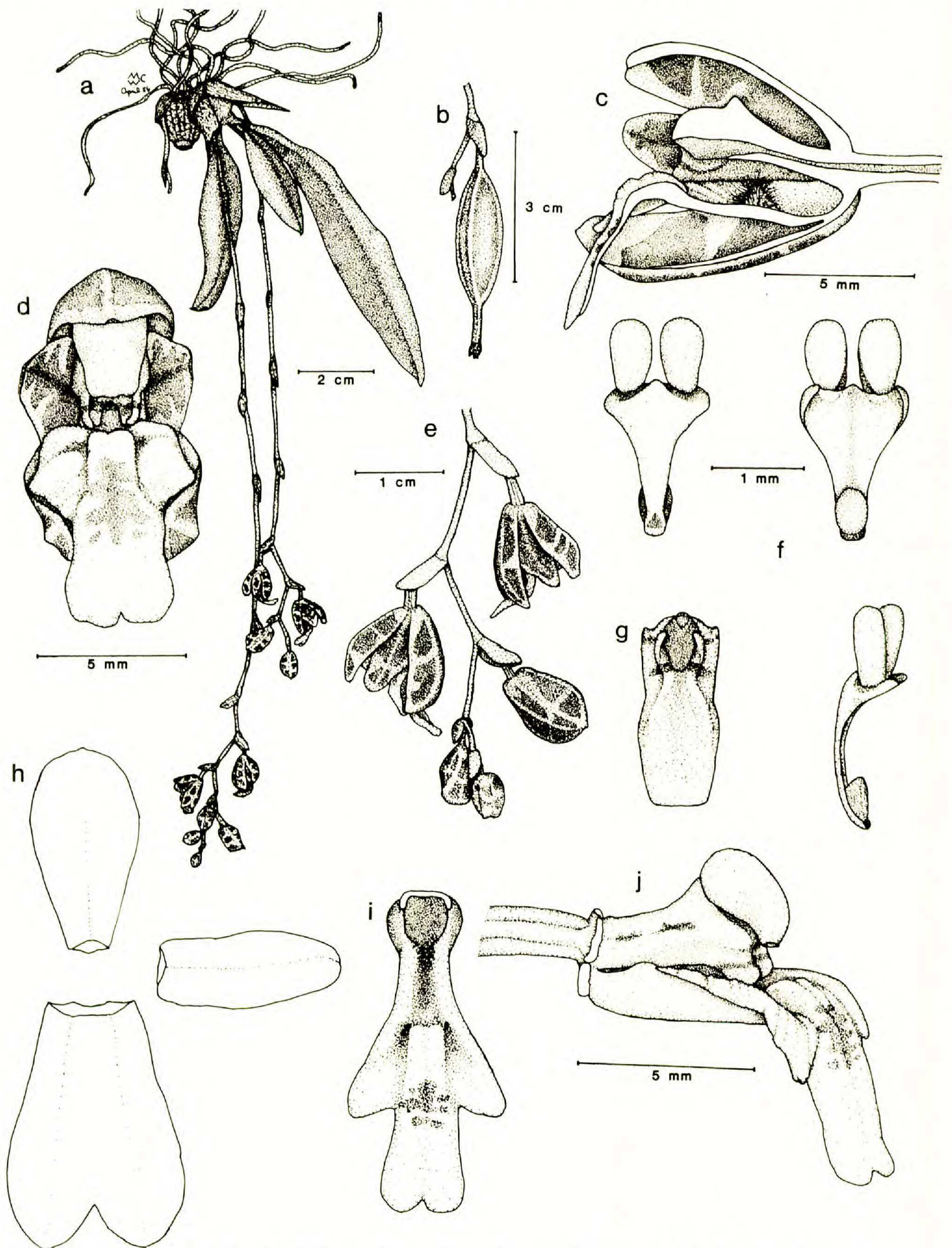


FIG. 17. *Goniochilus leochilinus*, Costa Rica (MWC84210). a. Habit. b. Capsule. c. Flower, longitudinal section. d. Flower, front view. e. Inflorescence habit. f. Pollinarium, three views: top, adaxial (l.) and abaxial (r.); bottom, side. g. Column (with anther cap removed), ventral view. h. Perianth outlines (exclusive of lip). i. Lip (flattened). j. Column and lip, side view (with sepals and petals removed).

et al. 23105 (MO); entre Dabagri y Sacabico y los bordes del mismo, fl, 7 Nov 1984, *Gómez et al.* 23301 (MO).

This species is easily distinguished by its red-purple suffused plants with weak, pendent inflorescences, pendent flowers, a trilobed lip bent in the middle, and a

basal hornless nectary. No other oncioid species could be confused with this distinctive plant.

After the type collection of *G. leochilinus* was made (it was described in 1871), it was not recollected until 1920, after which time it has been regularly encountered. My general impression is that it is much more common than the number of collections indicates. It is easily overlooked and grows on common plants where collectors are unlikely to search. Heller (personal notes at SEL) indicated that he frequently encountered the species in Nicaragua.

The species epithet means "smooth lip," an apparent reference to the lack of a complex, tuberculate, lip callus. On the type sheet in the Reichenbach Herbarium, this name appears after a crossed out one, "pantherina." Evidently, Reichenbach had originally given it this name, which would refer to the large, brown maculations of the perianth, and then changed his mind.

EXCLUDED NAME

Hybochilus huebneri Mansf., Repert. Spec. Nov. Regni Veg. 36: 61. 1934.—
TYPE: COLOMBIA. Vaupés, Río Negro Basin, El Castillo, near confluences of Guainía and Casiquiare, fl, 12 Dec 1942, *Schultes & López 9300* (neotype: AMES!). = *Polyotidium huebneri* (Mansf.) Garay, Bot. Mus. Leaf. 18: 105. 1958.

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